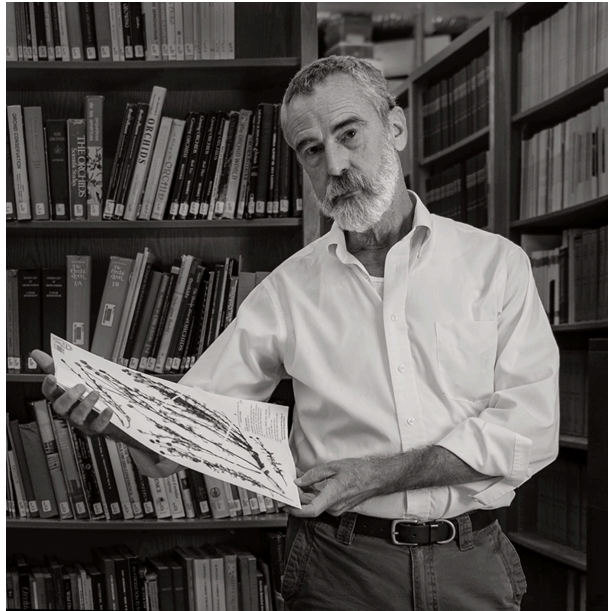


OBITUARY

WILLIAM MARK WHITTEN (1954–2019)



Florida Museum of Natural History. Photo by Kristen Grace.

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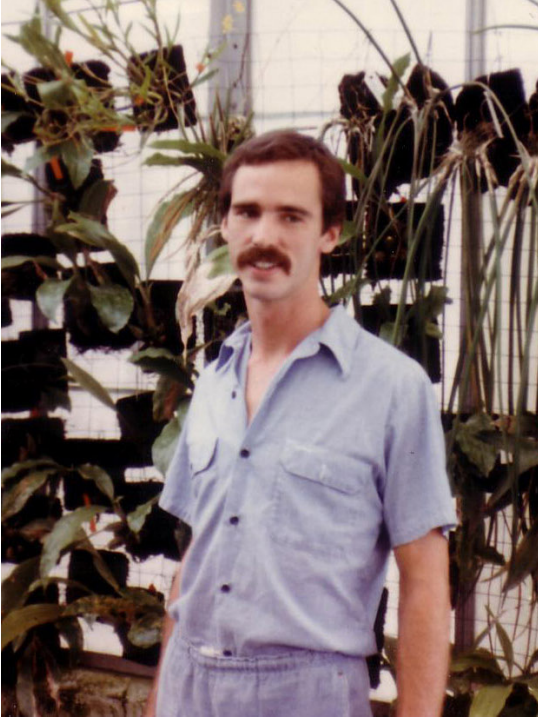
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On April 11, 2019, Dr. William Mark Whitten, a prolific neotropical orchid biologist passed away unexpectedly. He leaves an extensive corpus of work focused on (but not limited to) orchid pollination and systematics, and over four thousand beautifully prepared herbarium specimens. Everyone that met Mark can agree that he was a wonderful human being, kind to everyone, incredibly knowledgeable and yet very humble. Always of a calm demeanor, great sense of humor, and willingness to help, Mark

was an outstanding and relatable collaborator, and his publications (more than a hundred; see list below) are evidence of a productive and highly collaborative academic career.

Mark was born on October 20, 1954, in Memphis, Tennessee. His early education included Bishop Byrne High School in Memphis, where he graduated in 1972, and the Thomas More College in Crestview Hills, Kentucky, where he obtained a bachelor's degree in Biology in 1976. During college, he worked for various



Mark Whitten at Marie Selby Botanical Gardens greenhouse with living orchid research collection, 1982. Photographer unknown.

environmental consulting firms on the phytoplankton of the Ohio River. He pursued his graduate education and in 1979, he obtained his Master's degree in Botany from the University of Tennessee at Knoxville, with a thesis titled "Pollination ecology of *Monarda didyma*, *M. clinopodia* and hybrids (Lamiaceae) in the southern Appalachian Mountains", which, two years later, became his first publication.

In the same year Mark graduated from his Master's program, he started his doctoral degree at Florida State University in Tallahassee under the direction of Norris H. Williams. His research was centered on the pollination of orchids by euglossine bees. In 1981, Mark moved with the 'Williams Lab' to the Florida Museum of Natural History at the University of Florida in Gainesville. During this period, Mark also received the guidance of Robert L. Dressler (then at the Smithsonian Tropical Research Institute in Panama) and Calaway H. Dodson (then Executive Director of the Marie Selby Botanical Gardens in Sarasota, Florida). He spent the summer of 1981 as an intern at the Orchid Identification Center at the Marie



Mark Whitten in paramo El Angel, Carchi, Ecuador, holding an inflorescence of *Puya hamata* (Bromeliaceae) and *Espeletia pycnophylla* ssp. *angelensis* (Asteraceae) in the background, late 1980's. Photo: Mark Elliott.

Selby Botanical Gardens. In 1985 he defended his dissertation, titled "Variation in floral fragrances and pollinators in the *Gongora quinquenervis* complex (Orchidaceae) in central Panama".

For his dissertation, Mark learned techniques of gas chromatography and mass spectrometry for the isolation and identification of the chemical compounds produced by flowers of *Gongora* and other orchid genera, responsible for the attraction of their euglossine bee pollinators. He became part of a small group of orchid researchers (including Dressler, Dodson, Williams and James Ackerman) that made substantial contributions to the understanding of the biology of orchid bees. During this period, Mark collected a substantial amount of bee specimens and gathered data and observations that he later shared and published in collaboration with other orchid bee experts. Some interesting anecdotes of Mark's research during this period are presented in Allen Young's book "Sarapiquí Chronicle: A Naturalist in Costa Rica" (1991. Smithsonian Institution Press).



Mark Whitten in the lava flows of Paramo de La Virgen, Napo, Ecuador in 2009. Photographer unknown.



Mark Whitten at Ordway-Swisher Biological Station in Florida, 2014, holding *Toxicodendron radicans* (Anacardiaceae). Photo: Kurt Neubig

After obtaining his Ph.D., Mark continued working at the Florida Museum of Natural History, initially as a postdoctoral research associate and later as Senior Biological Scientist. He expanded his professional skills by learning molecular systematic techniques and phylogenetics with Mark W. Chase (first in 1990 at the University of North Carolina in Chapel Hill, and later in 1994 at the Jodrell Laboratory of the Royal Botanic Gardens, Kew). Mark Whitten, Mark Chase and Norris Williams collaborated for many years thereafter, assembling phylogenies for a variety of orchid groups. Mark described or co-described several orchid species in the genera *Basiphyllaea* (1 sp.), *Gongora* (5 spp.), *Ornithidium* (1 sp.), *Solenidium* (1 sp.) and *Stanhopea* (1 sp.), and also one species of *Pitcairnia* (Bromeliaceae). He also co-described two orchid genera (*Brasilocycnis* G. Gerlach & Whitten and *Nohawilliamsia* M.W. Chase & Whitten) and one subgenus (*Houlletia* subgen. *Neohoulletia* G. Gerlach & Whitten). He also authored and co-authored numerous generic transfers. Mark discovered or documented many other new orchid species and genera, but frequently gave them

to other specialists or students for their description and publication. Four orchid species are named after him: *Epidendrum whittenii* Hágsater & Dodson, *Lepanthes whittenii* Pupulin & Bogarín, *Maxillaria whittenii* Dodson and *Stanhopea whittenii* Soto-Arenas, Salazar & G. Gerlach.

For most of his time in the Florida Museum of Natural History, Mark was in charge of the Molecular Lab associated with the University of Florida Herbarium (FLAS), a position he held until 2015. In that year, he became a member of the Scientific Committee of *Lankesteriana*, the academic journal of the Lankester Botanical Garden. In 2013, he and collaborators began a floristic inventory and DNA barcoding of the Ordway-Swisher Biological Station in Putnam County, Florida, which he continued until his death. In most recent years, Mark collaborated with Pam and Doug Soltis in a variety of projects, including their US-China Dimensions of Biodiversity project, experimenting with isolation methods for high molecular weight DNA suitable for genome sequencing, gulf coast biodiversity hotspot studies, etc.

Mark was a great mentor for numerous students from the University of Florida, and other institutions alike. He had an encyclopedic knowledge of natural history and he shared it with students and colleagues in a very constructive and encouraging manner. Mark cared deeply for students' academic progress as well as their personal well-being. He was especially generous with international students; he would take time and care in helping them navigate through differences in culture, all while maintaining a sense of humor that made them feel right at home. Mark was fully aware of the challenges faced in academia by students, and he set a high standard of integrity, honesty, and generosity that we all should emulate.

As a group of his former students, we in particular owe Mark a great deal for his help in our academic development and for our career success. He liked to turn a phrase in Latin, and this one meant a lot to him: “*Ubi caritas et amor, Deus ibi est.*”

OTHER OBITUARIES FOR W. MARK WHITTEN

- Blanco, M.A., M. Chase, L. Endara, T. Mirenda & K.M. Neubig (2019). Dr. William Mark Whitten (1954–2019). *Orchids (Bulletin of the American Orchid Society)* 88(6): 419–420.
- Gerlach, G. (2019). Mark Whitten (1954–2019). *OrchideenJournal* (in press).
- Pridgeon, A. (2019). William Mark Whitten (1954–2019). *Orchid Research Newsletter* 74: 7–9.

PUBLICATIONS BY W. MARK WHITTEN

1. **Whitten, W.M.** (1981). Pollination ecology of *Monarda didyma*, *M. clinopodia*, and hybrids (Lamiaceae) in the southern Appalachian Mountains. *American Journal of Botany* 68(3): 435–442.
2. Caponetti, J.D., **W.M. Whitten** & M.J. Beck (1982). Axenic culture and induction of callus and sporophytes of the Appalachian *Vittaria* gametophyte. *American Fern Journal* 72: 36–40.
3. Williams, N.H. & **W.M. Whitten** (1982). Identification of floral fragrance components of *Stanhopea embreei* and attraction of its pollinator to synthetic fragrance compounds. *American Orchid Society Bulletin* 51: 1262–1266.
4. Williams, N.H. & **W.M. Whitten** (1983). Orchid floral fragrances and male euglossine bees: methods and advances in the last sesquidecade. *Biological Bulletin* 164: 355–395.
5. Williams, N.H., **W.M. Whitten** & C.H. Dodson (1984). Preliminary analyses of the floral fragrances of species of *Acineta*, *Houlettia*, *Luddemannia*, *Lycomormium*, *Paphinia*, and *Sievekingia* (Orchidaceae). *Selbyana* 7(2/4): 315–317.
6. **Whitten, W.M.** (1985). Floral fragrances and pollinators of the *Gongora quinquenervis* R. & P. complex (Orchidaceae) in central Panama. (Abstract of talk presented at the Annual Meetings of the Botanical Society of America, Gainesville, Florida, 11–15 August 1985). *American Journal of Botany* 72(6): 916.
7. Williams, N.H., **W.M. Whitten** & L.F. Pedrosa (1985). Crystalline production of fragrance in *Gongora quinquenervis*. *American Orchid Society Bulletin* 54: 598–603.
8. McClure, G.L., N.H. Williams & **W.M. Whitten** (1985). Orchids and Bee's Knees: investigating the euglossine syndrome with Gas Chromatography/Fourier Transform Infrared GC/FT-IR. *Proceedings of the 1985 International Conference on Fourier and Computerized Infrared Spectroscopy, Ottawa, Canada*, Volume 0553: 355.
9. **Whitten, W.M.**, N.H. Williams, W.S. Armbruster, M.A. Battiste, L. Strekowski & N. Lindquist (1985). Carvone oxide: an example of convergent evolution in euglossine pollinated plants. *Systematic Botany* 11(1): 222–228.
10. Lindquist, N., M.A. Battiste, **W.M. Whitten**, N.H. Williams & L. Strekowski (1985). Trans-carvone oxide, a monoterpene epoxide from the fragrance of *Catasetum*. *Phytochemistry* 24(4): 863–865.
11. Stern, W.L., K.J. Curry & **W.M. Whitten** (1986). Staining fragrance glands in orchid flowers. *Bulletin of the Torrey Botanical Club* 113(3): 288–297.
12. Hills, H.G., N.H. Williams & **W.M. Whitten** (1986). Cyclic fragrance production in euglossine pollinated orchids. (Conference Abstract). *American Journal of Botany* 73(5): 727.
13. Williams, N.H. & **W.M. Whitten** (1988). *Stanhopea panamensis*, a new species from central Panama. *Lindleyana* 3(1): 9–11.
14. **Whitten, W.M.**, H.G. Hills & N.H. Williams (1988). Occurrence of ipsdienol in floral fragrances. *Phytochemistry* 27(9): 2759–2760.
15. Dodson, C.H., N.H. Williams & **W.M. Whitten** (1989). A new species of *Gongora* (Orchidaceae) from Ecuador. *Lindleyana* 4(1): 30–52.
16. Huck, R.B., W.S. Judd, **W.M. Whitten**, J.D. Skean, R.P. Wunderlin & K.R. Delaney (1989). A new *Dicerandra* (Labiatae) from the Lake Wales Ridge of Florida, with a cladistic analysis and discussion of endemism. *Systematic Botany* 14(2): 197–213.

17. **Whitten, W.M.**, A.M. Young & N.H. Williams (1989). Function of glandular secretions in fragrance collection by male euglossine bees (Apidae: Euglossini). *Journal of Chemical Ecology* 15(4): 1285–1295.
18. **Whitten, W.M.** & N.H. Williams (1991). A new species and nomenclatural changes in *Gongora* Sect. *Acropera* (Orchidaceae: Stanhopeinae). *Lindleyana* 6(2): 109–112.
19. **Whitten, W.M.** & N.H. Williams (1991). *Gongora escobariana* Whitten, a new species from Colombia, and the rediscovery of *G. sanderiana* in Peru. *Orquideología* 18(2): 105–127.
20. Dressler, R.L. & **W.M. Whitten** (1991). *Kegeliella*. *American Orchid Society Bulletin* 60: 684–687.
21. **Whitten, W.M.** & N.H. Williams (1992). Floral fragrances of *Stanhopea* (Orchidaceae). *Lindleyana* 7: 130–153.
22. Luther, H.E. & **W.M. Whitten** (1992). A new *Pitcairnia* from western Ecuador. *Journal of the Bromeliad Society* 42(6): 245–247.
23. **Whitten, W.M.**, A.M. Young & D.L. Stern (1993). Nonfloral sources of chemicals that attract male euglossine bees (Apidae: Euglossini). *Journal of Chemical Ecology* 19(12): 3017–3027. Erratum: (1994) 20(3): 821–822.
24. Christenson, E.A. & **W.M. Whitten** (1995). *Phalaenopsis bellina* (Rchb.f.) Christenson, a segregate from *P. violacea* Witte (Orchidaceae: Aeridinae). *Brittonia* 47(1): 57–60.
25. Eltz, T., D. Roubik, **W.M. Whitten** & K.E. Linsenmair (1999). Fragrance collection: storage and accumulation by individual male orchid bees. *Journal of Chemical Ecology* 25(1): 157–176.
26. Cameron, K.M., M.W. Chase, **W.M. Whitten**, P.J. Kores, D. Jarrell, V.A. Albert, T. Yukawa, H.G. Hills & D.H. Goldman (1999). A phylogenetic analysis of the Orchidaceae: evidence from *rbcl* nucleotide sequences. *American Journal of Botany* 86(2): 208–224.
27. **Whitten, W.M.**, N.H. Williams & K.V. Glover (1999). Sulphuryl fluoride fumigation: effect on DNA extraction and amplification from herbarium specimens. *Taxon* 48(3): 507–510.
28. Gerlach, G. & **W.M. Whitten** (1999). *Brasilocycnis*, eine neue Gattung der Subtribus Stanhopeinae. *Journal für den Orchideenfreund* 6: 188–192.
29. Hills, H.G., N.H. Williams & **W.M. Whitten** (1999). Chapter 10: Fragrances of Catasetums. In: A.W. Holst. *The World of Catasetums*. Timber Press, Portland, pp. 263–272.
30. Ryan, A., **W.M. Whitten**, M.A.T. Johnson & M.W. Chase (2000). A phylogenetic assessment of *Lycaste* and *Anguloa* (Orchidaceae: Maxillarieae). *Lindleyana* 15(1): 33–45.
31. Savolainen, V., M.F. Fay, D.C. Albach, A. Backlund, M. van der Bank, K.M. Cameron, S.A. Johnson, M.D. Lledó, J.C. Pintaud, M. Powell, M.C. Sheahan, D.E. Soltis, P.S. Soltis, P. Weston, **W.M. Whitten**, K.J. Wurdack & M.W. Chase (2000). Phylogeny of the eudicots: a nearly complete familial analysis based on *rbcl* gene sequences. *Kew Bulletin* 55(2): 257–309.
32. van den Berg, C., W. Higgins, R.L. Dressler, **W.M. Whitten**, A. Culham & M.W. Chase (2000). A phylogenetic analysis of Laeliinae (Orchidaceae) based on sequence data from Internal Transcribed Spacers (ITS) of nuclear ribosomal DNA. *Lindleyana* 15(2): 96–114.
33. Wood, T.H., **W.M. Whitten** & N.H. Williams (2000). Phylogeny of *Hedychium* and related genera (Zingiberaceae) based on ITS sequence data. *Edinburgh Journal of Botany* 57(2): 261–270.
34. **Whitten, W.M.**, N.H. Williams & M.W. Chase (2000). Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. *American Journal of Botany* 87(12): 1842–1856.
35. Ackerman, J.D., R.L. Tremblay & **W.M. Whitten** (2001). Notes on the Caribbean orchid flora. III. New species of *Basiphyllaea* and *Lepanthes*. *Lindleyana* 16(1): 13–16.
36. Sosa, V., M.W. Chase, G. Salazar, **W.M. Whitten** & N.H. Williams (2001). Phylogenetic position of *Dignathe* (Orchidaceae: Oncidiinae): evidence from nuclear ITS ribosomal DNA sequences. *Lindleyana* 16(2): 94–101.
37. Williams, N.H., M.W. Chase, T. Fulcher & **W.M. Whitten** (2001). Molecular systematics of the Oncidiinae based on evidence from four DNA sequence regions: expanded circumscriptions of *Cyrtochilum*, *Erycina*, *Otoglossum*, and *Trichocentrum* and a new genus (Orchidaceae). *Lindleyana* 16(2): 113–139.
38. Williams, N.H. & **W.M. Whitten** (2001). Checking an orchid hybrid's background: the use of molecular data in determining parentage of hybrids. *Orchids (Bulletin of the American Orchid Society)* 70: 1056–1061.
39. Williams, N.H., M.W. Chase & **W.M. Whitten** (2001). Phylogenetic positions of *Miltoniopsis*, *Caucaea*, a new genus, *Cyrtochiloides*, and *Oncidium phymatochilum* (Orchidaceae: Oncidiinae) based on nuclear and plastid DNA sequence data. *Lindleyana* 16(4): 272–285.
40. Iudica, C.A., **W.M. Whitten** & N.H. Williams (2001). Small bones from dried mammal museum specimens as a reliable source of DNA. *BioTechniques* 30(4): 732–734, 736.
41. Goldman, D.H., J.V. Freudenstein, P.J. Kores, M. Molvray, D.C. Jarrell, **W.M. Whitten**, K.M. Cameron, R.K. Jansen &

- M.W. Chase (2001). Phylogenetics of Arethuseae (Orchidaceae) based on plastid matK and rbcL sequences. *Systematic Botany* 26(3): 670–695.
42. Zomlefer, W.B., N.H. Williams, **W.M. Whitten** & W.S. Judd (2001). Generic circumscription and relationships in the Tribe Melanthieae (Liliales, Melanthiaceae), with emphasis on *Zigadenus*: evidence from ITS and trnL-F sequence data. *American Journal of Botany* 88(9): 1657–1669.
 43. van den Berg, C., W. Higgins, R.L. Dressler, **W.M. Whitten**, A. Culham & M.W. Chase (2002). Molecular systematics of the Laeliinae. In: J. Clark, W. Elliott, G. Tingley & J. Biro (eds.) *Proceedings of the 16th World Orchid Conference, Vancouver, 1999*, pp. 170–176.
 44. Chase, M.W., N.H. Williams & **W.M. Whitten** (2002). DNA phylogenetics and the *Oncidium* alliance: what to do with the Odontoglossums? In: J. Clark, W. Elliott, G. Tingley & J. Biro (eds.) *Proceedings of the 16th World Orchid Conference, Vancouver, 1999*, pp. 419–420.
 45. **Whitten, W.M.**, N.H. Williams & M.W. Chase (2002). Molecular phylogenetics of the Maxillarieae. In: J. Clark, W. Elliott, G. Tingley & J. Biro (eds.) *Proceedings of the 16th World Orchid Conference, Vancouver, 1999*, p. 429.
 46. Koehler, S., N.H. Williams, **W.M. Whitten** & M.C.E. Amaral (2002). Phylogeny of the *Bifrenaria* (Orchidaceae) complex based on morphology and sequence data from nuclear rDNA Internal Transcribed Spacers (ITS) and chloroplast trnL-trnF region. *International Journal of Plant Sciences* 163(6): 1055–1066.
 47. Higgins, W., C. van den Berg, **W.M. Whitten** (2002). A combined molecular phylogeny of *Encyclia* (Orchidaceae) and relationships within Laeliinae. *Selbyana* 24(2): 165–179.
 48. Carlswald, B.S., **W.M. Whitten** & N.H. Williams (2003). Molecular phylogenetics of Neotropical leafless Angraecinae (Orchidaceae): reevaluation of generic concepts. *International Journal of Plant Sciences* 164(1): 43–51.
 49. Dalström, S. & **W.M. Whitten** (2003). A new species of *Solenidium* (Orchidaceae) from Ecuador. *Lankesteriana* 6(1): 1–4.
 50. Carnevali, G., J.L. Tapia, N.H. Williams & **W.M. Whitten** (2003). Sistemática, filogenia y biogeografía de *Myrmecophila* (Orchidaceae). *Lankesteriana* 7(1): 29–32.
 51. Ojeda, I., G. Carnevali, N.H. Williams & **W.M. Whitten** (2003). Phylogeny of the *Heterotaxis* Lindley complex (Maxillariinae): evolution of the vegetative architecture and pollination syndromes. *Lankesteriana* 7(1): 45–47.
 52. Williams, N.H. & **W.M. Whitten** (2003). Molecular phylogenetics and generic concepts in the Maxillarieae (Orchidaceae). *Lankesteriana* 7(1): 61–62.
 53. Zomlefer, W.B., **W.M. Whitten**, N.H. Williams & W.S. Judd (2003). An overview of *Veratrum s.l.* (Liliales: Melanthiaceae) and an infrageneric phylogeny based on ITS sequence data. *Systematic Botany* 28(2): 250–269.
 54. Eltz, T., D. Roubik & **W.M. Whitten** (2003). Fragrances, male display and mating behaviour of *Euglossa hemichlora*: a flight cage experiment. *Physiological Entomology* 28(4): 251–260.
 55. Dressler, R.L., **W.M. Whitten** & N.H. Williams (2004). Phylogenetic relationships of *Scaphyglottis* and related genera (Laeliinae: Orchidaceae) based on nrDNA ITS sequence data. *Brittonia* 56(1): 58–66.
 56. **Whitten, W.M.** (2004). Book review: *Native Ecuadorian Orchids Volume IV* by Calaway H. Dodson [2003. Dodson Trust, 232 pp.]. *Orchids (Bulletin of the American Orchid Society)* 73(2): 142.
 57. Chase, M.W., L. Hanson, V.A. Albert, **W.M. Whitten** & N.H. Williams (2005). Life history evolution and genome size in Subtribe Oncidiinae (Orchidaceae). *Annals of Botany* 95(1): 191–199.
 58. **Whitten, W.M.**, N.H. Williams, R.L. Dressler, G. Gerlach & F. Pupulin (2005). Generic relationships of Zygopetalinae (Orchidaceae: Cymbidieae): combined molecular evidence. *Lankesteriana* 5(2): 87–107.
 59. Loayza, M.D., N.H. Williams & **W.M. Whitten** (2005). *Phragmipedium kovachii*: molecular systematics of a New World orchid. *Orchids (Bulletin of the American Orchid Society)* 74(2): 132–137.
 60. Williams, N.H., **W.M. Whitten** & R.L. Dressler (2005). Molecular systematics of *Telipogon* (Orchidaceae: Oncidiinae) and its allies: nuclear and plastid DNA sequence data. *Lankesteriana* 5(3): 163–184.
 61. **Whitten, W.M.** & N.H. Williams (2005). Evolutionary relationships within tribe Maxillarieae: lessons from molecules, morphology, and pollination biology. In: A. Raynal-Roques & A. Roguenant (eds.), *Actes du 18e Congrès Mondial et Exposition d'Orchidées, 11–20 mars 2005. France Orchidées*, Naturalia Publications, Turriers, France, p. 604.
 62. Zomlefer, W.B., W.S. Judd, **W.M. Whitten** & N.H. Williams (2006). A synopsis of Melanthiaceae (Liliales) with focus on character evolution in Tribe Melanthieae. *Aliso* 22(1): 566–578.
 63. Carlswald, B.S., **W.M. Whitten**, N.H. Williams & B. Bytebier (2006). Molecular phylogenetics of Vandeeae (Orchidaceae) and the evolution of leaflessness. *American Journal of Botany* 93(5): 770–786.
 64. Zomlefer, W.B., **W.M. Whitten**, N.H. Williams & W.S. Judd (2006). Infrageneric phylogeny of *Schoenocaulon* (Liliales: Melanthiaceae) with clarification of cryptic species based on ITS sequence data and geographical distribution. *American Journal of Botany* 93(8): 1178–1192.

65. **Whitten, W.M.**, M.A. Blanco & N.H. Williams (2006). Recircumscription of *Pityphyllum* (Orchidaceae: Maxillariinae). *Orchids (Bulletin of the American Orchid Society)* 75(3): 451–456.
66. Blanco, M.A., **W.M. Whitten**, D.S. Penneys, N.H. Williams, K.M. Neubig & L. Endara (2006). A simple and safe method for rapid drying of plant specimens using forced-air space heaters. *Selbyana* 27(1): 83–87.
67. Blanco, M.A., **W.M. Whitten**, N.H. Williams & S. Koehler (2006). Capillitial extrusion from fruits of *Maxillaria nardoides* (Orchidaceae: Maxillariinae). *Orchids (Bulletin of the American Orchid Society)* 75(9): 677–683.
68. **Whitten, W.M.** & B.S. Carlswald (2006). Ghosts of the Caribbean: *Dendrophylax fawcettii* and an overview of the genus. *Orchids (Bulletin of the American Orchid Society)* 75(10): 742–746.
69. **Whitten, W.M.** & B.S. Carlswald (2006). *Dendrophylax* species. *Orchids (Bulletin of the American Orchid Society)* 75(10): 748–749.
70. **Whitten, W.M.** & B.S. Carlswald (2006). A comparison of *Dendrophylax* and *Campylocentrum*. *Orchids (Bulletin of the American Orchid Society)* 75(10): 748–749.
71. Blanco, M.A., K.M. Neubig & **W.M. Whitten** (2007). A new *Maxillaria* (Orchidaceae) from Panama and Colombia, and a Brazilian species found in Ecuador. *Orchids (Bulletin of the American Orchid Society)* 76(6): 451–456.
72. Ionta, G.M., W.S. Judd, N.H. Williams & **W.M. Whitten** (2007). Phylogenetic relationships in *Rhexia* (Melastomataceae): evidence from DNA sequence data and morphology. *International Journal of Plant Sciences* 168(7): 1055–1066.
73. **Whitten, W.M.**, M.A. Blanco, N.H. Williams, S. Koehler, G. Carnevali, R.B. Singer, L. Endara & K.M. Neubig (2007). Molecular phylogenetics of *Maxillaria* and related genera (Orchidaceae: Cymbidieae) based on combined molecular data sets. *American Journal of Botany* 94(11): 1860–1889 (+ front cover).
74. Blanco, M.A., G. Carnevali, **W.M. Whitten**, R.B. Singer, S. Koehler, N.H. Williams, I. Ojeda, K.M. Neubig & L. Endara (2007). Generic realignments in Maxillariinae (Orchidaceae). *Lankesteriana* 7: 515–537.
75. Blanco, M.A., G. Carnevali, **W.M. Whitten**, R.B. Singer, S. Koehler, N.H. Williams, I. Ojeda, K.M. Neubig & L. Endara (2008). Generic realignments in Maxillariinae (Orchidaceae): corrigenda et addenda. *Lankesteriana* 8: 15.
76. Stern, W.L. & **W.M. Whitten** (2008). Comparative vegetative anatomy of Stanhopeinae (Orchidaceae). *Botanical Journal of the Linnean Society* 129(2): 87–103.
77. Koehler, S., J.S. Cabral, **W.M. Whitten**, N.H. Williams, R.B. Singer, K.M. Neubig, M. Guerra, A.P. de Souza & M.C.E. Amaral (2008). Molecular phylogeny of the Neotropical genus *Christensonella* (Orchidaceae, Maxillariinae): species delimitation and insights into chromosome evolution. *Annals of Botany* 102(4): 491–507.
78. Carlswald, B.S. & **W.M. Whitten** (2008). The correct genus for the jingle bell orchid, *Harrisella porrecta*. *North American Native Orchid Journal* 14: 272–274.
79. N.H. Williams & **W.M. Whitten** (2008). Molecular phylogeny and floral fragrances of male euglossine bee-pollinated orchids: a study of *Stanhopea* (Orchidaceae). *Plant Species Biology* 14(2): 129–136.
80. Chase, M.W., N.H. Williams, K.M. Neubig & **W.M. Whitten** (2008). Taxonomic transfers in Oncidiinae to accord with *Genera Orchidacearum, Vol. 5. Orchids (Bulletin of the American Orchid Society)* 77(12): 20–31.
81. **Whitten, W.M.** (2009). Book review: *Huntleyas and Related Orchids*. [P.A. Harding (2008). Timber Press, 260 pp.] *Orchids (Bulletin of the American Orchid Society)* 78(3): 176.
82. Chase, M.W., N.H. Williams & **W.M. Whitten** (2009). Oncidiinae nomenclature: generic changes in *Genera Orchidacearum, Volume 5. Orchids (Bulletin of the American Orchid Society)* 78(4): 228–238.
83. **Whitten, W.M.** (2009). *Nohawilliamsia*: a new genus honors Norris H. Williams, Ph.D. *Orchids (Bulletin of the American Orchid Society)* 78(9): 552–555.
84. **Whitten, W.M. et al.** (2009). Subtribe Maxillariinae. In: A.M. Pridgeon, P.J. Cribb, M.W. Chase & F.N. Rasmussen (eds.). *Genera Orchidacearum, Volume 5. Epidendroideae (Part two)*. Oxford University Press, Oxford, UK. Pp. 119–211.
85. Neubig, K.M., **W.M. Whitten**, B.S. Carlswald, M.A. Blanco, L. Endara, N.H. Williams & M. Moore (2009). Phylogenetic utility of *ycf1* in orchids: a plastid gene more variable than *matK*. *Plant Systematics and Evolution* 277: 75–84.
86. Chase, M.W., N.H. Williams, A.D. de Faria, K.M. Neubig, M.C.E. Amaral & **W.M. Whitten** (2009). Floral convergence in Oncidiinae (Cymbidieae; Orchidaceae): an expanded concept of *Gomesa* and a new genus *Nohawilliamsia*. *Annals of Botany* 104(3): 387–402.
87. van den Berg, C., W. Higgins, R.L. Dressler, **W.M. Whitten**, M.A. Soto-Arenas & M.W. Chase (2009). A phylogenetic study of Laeliinae (Orchidaceae) based on combined nuclear and plastid DNA sequences. *Annals of Botany* 104(3): 417–430.
88. Neubig, K.M., N.H. Williams, **W.M. Whitten** & F. Pupulin (2009). Molecular phylogenetics and the evolution of fruit and leaf morphology of *Dichaea* (Orchidaceae: Zygopetalinae). *Annals of Botany* 104(3): 457–467.

89. **Whitten, W.M.** (2009). Norris Williams [Biographical sketch]. In: T. Kull, J. Arditti & S.M. Wong (eds.), *Orchid Biology: Reviews and Perspectives, X*, Springer, Pp. xii–xiii.
90. Ackerman, J.D. & **W.M. Whitten** (2010). A new *Ornithidium* (Orchidaceae: Maxillariinae) from the Massif de la Hotte of Haiti. *Lankesteriana* 9(3): 509–512.
91. Gajdeczka, M.T., K.M. Neubig, W.S. Judd, **W.M. Whitten**, N.H. Williams & K.D. Perkins (2010). Phylogenetic analyses of the *Gaylussacia frondosa* complex (Ericaceae: Vaccinieae) based on molecular and morphological characters. *Journal of the Botanical Research Institute of Texas* 4(1): 245–260.
92. Silvera, K., K.M. Neubig, **W.M. Whitten**, N.H. Williams, K. Winter & J.C. Cushman (2010). Evolution along the crassulacean acid metabolism continuum. *Functional Plant Biology* 37: 995–1010.
93. Chase, M.W. & **W.M. Whitten** (2011). Further taxonomic transfers in Oncidiinae (Orchidaceae). *Phytotaxa* 20: 26–32.
94. Endara, L., N.H. Williams & **W.M. Whitten** (2011). Filogenia molecular preliminar de *Scaphosepalum* (Orchidaceae: Pleurothallidinae). *Lankesteriana* 11(3): 245–252.
95. Neubig, K.M., **W.M. Whitten**, M.A. Blanco, L. Endara, N.H. Williams & S. Koehler (2011). Preliminary molecular phylogenetics of *Sobralia* and relatives (Orchidaceae: Sobralieae). *Lankesteriana* 11(3): 307–317.
96. **Whitten, M.W.** & M.A. Blanco (2011). Defining generic limits in *Maxillaria*. *Orchids (Bulletin of the American Orchid Society)* 80(2): 104–113.
97. Carnevali, G., W. Cetzal-Ix & **W.M. Whitten** (2012). *Cryptocentrum beckendorffii* (Orchidaceae: Maxillariinae), an extraordinary new species from Andean Peru. *Phytotaxa* 68: 45–51.
98. Neubig, K.M., **W.M. Whitten**, N.H. Williams, M.A. Blanco, L. Endara, G. Burleigh, K. Silvera, J.C. Cushman & M.W. Chase (2012). Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets. *Botanical Journal of the Linnean Society* 168: 117–146.
99. **W.M. Whitten**, C.C. Jacono & N.S. Nagalingum (2012). An expanded plastid phylogeny of *Marsilea* with emphasis on North American species. *American Fern Journal* 102(2): 114–135.
100. Papadopulos, A.S.T., M.P. Powell, F. Pupulin, J. Warner, J.A. Hawkins, N. Salamin, L. Chittka, N.H. Williams, **W.M. Whitten**, D. Loader, L.M. Valente, M.W. Chase & V. Savolainen (2013). Convergent evolution of floral signals underlies the success of Neotropical orchids. *Proceedings of the Royal Society B: Biological Sciences* 280(1765): 20130960.
101. Neubig, K.M., **W.M. Whitten**, J.R. Abbott, S. Elliott, D.E. Soltis & P.S. Soltis (2014). Variables affecting DNA preservation in archival plant specimens. In: W.L. Applequist & L.M. Campbell (eds.), *DNA banking in the 21st Century: Proceedings of the U.S. workshop on DNA banking*. The William L. Brown Center at the Missouri Botanical Garden, St. Louis, pp. 81–136.
102. Neubig, K.M., F. Herrera, S. Manchester, C.C. Germain-Aubrey, R. Abbott & **W.M. Whitten** (2014). Systematics of Ulmaceae and placement of the extinct *Cedrelospermum*. *The Paleontological Society Special Publications* 13: 18–19.
103. **W.M. Whitten**, K.M. Neubig & N.H. Williams (2014). Generic and subtribal relationships in Neotropical Cymbidieae (Orchidaceae) based on matK/ycf1 plastid data. *Lankesteriana* 13(3): 375–392.
104. Neubig, K.M., B.S. Carlswald, **W.M. Whitten** & N.H. Williams (2015). Nectary structure and nectar in *Sobralia* and *Elleanthus* (Sobralieae: Orchidaceae). *Lankesteriana* 15(2): 113–127.
105. Neubig, K.M., O. Blanchard, **W.M. Whitten** & S.F. McDaniel (2015). Molecular phylogenetics of *Kosteletzkya* (Malvaceae, Hibisceae) reveals multiple independent and successive polyploid speciation events. *Botanical Journal of the Linnean Society* 179(3): 421–435.
106. Givnish, T.J., D. Spalink, M. Ames, S.P. Lyon, S.J. Hunter, A. Zuluaga, W.D.J. Iles, M.A. Clements, M.T.K. Arroyo, J. Leebens-Mack, L. Endara, R. Kriebel, K.M. Neubig, **W.M. Whitten**, N.H. Williams & K.M. Cameron (2015). Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society B: Biological Sciences* 282(1814): 20151553.
107. Kim, H.T., J.S. Kim, M.J. Moore, K.M. Neubig, N.H. Williams, **W.M. Whitten** & J.H. Kim (2015). Seven new complete plastome sequences reveal rampant independent loss of the ndh gene family across orchids and associated instability of the Inverted Repeat/Small Single-Copy Region boundaries. *PLoS ONE* 10(11): e0142215.
108. **Whitten, W.M.** (2015). Orchid pollination 150 years after Darwin. [Book review of R. Edens-Meier & P. Bernhardt (eds.). (2014). *Darwin's orchids: then and now*. University of Chicago Press, xi + 419 pp.]. *Ecology* 96(7): 2030–2031.
109. Pérez-Escobar, O.A., M. Gottschling, **W.M. Whitten**, G. Salazar & G. Gerlach (2016). Sex and the Catasetinae (Darwin's favourite orchids). *Molecular Phylogenetics and Evolution* 97: 1–10.
110. Molgo, I.E., G. Carnevali Fernández-Concha, **W.M. Whitten** & N.H. Williams (2016). *Dendrophylax megarhizus* (Orchidaceae), a new species from Mexico. *Systematic Botany* 41(2): 263–274.

111. Pastore, J.F.B., J.R. Abbott, K.M. Neubig, **W.M. Whitten**, R.B. Mascarenhas, M.C.A. Mota & C. van den Berg (2017). A molecular phylogeny and taxonomic notes in *Caamembeca* (Polygalaceae). *Systematic Botany* 42(1): 54–62.
112. Pessoa, E.M., J. Viruel, M.V. Alves, D. Bogarín-Chaves, **W.M. Whitten**, M.J.M. Christenhusz & M.W. Chase (2018). Evolutionary history and systematics of *Campylocentrum* (Orchidaceae: Vandaeae: Angraecinae): a phylogenetic and biogeographical approach. *Botanical Journal of the Linnean Society* 186(2): 158–178.
113. Salazar, G.A., J.A.N. Batista, L.I. Cabrera, C. van den Berg, **W.M. Whitten**, E.C. Smidt, C.R. Buzatto, R.B. Singer, G. Gerlach, R. Jiménez-Machorro, J.A. Radins, I.S. Insaurrealde, L.R.S. Guimarães, F. de Barros, F. Tobar, J.L. Linares, E. Mújica, R.L. Dressler, M.A. Blanco, E. Hágsater & M.W. Chase (2018). Phylogenetic systematics of subtribe Spiranthinae (Orchidaceae: Orchidoideae: Cranichideae) based on nuclear and plastid DNA sequences of a nearly complete generic sample. *Botanical Journal of the Linnean Society* 186(3): 273–303.
114. Smidt, E.C., A.L.V. Toscano de Brito, A.C. Martins, C.A. Royer, **W.M. Whitten** & M.W. Chase (2018). Phylogenetics, biogeography and character evolution in the *Ornithocephalus* clade (Orchidaceae, Oncidiinae). *Botanical Journal of the Linnean Society* 188(4): 339–354.
115. Allen, J.M., C.C. Germain-Aubrey, N. Barve, K.M. Neubig, L.C. Majure, S.W. Laffan, B.D. Mishler, H.L. Owens, S.A. Smith, **W.M. Whitten**, J.R. Abbott, D.E. Soltis, R. Guralnick & P.S. Soltis (2019). Spatial phylogenetics of Florida vascular plants: the effects of calibration and uncertainty on diversity estimates. *iScience* 11: 57–70.

